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Seepiophila jonesi, a new genus and species of vestimentiferan tube worm (Annelida: Pogonophora) from hydrocarbon seep communities in the Gulf of Mexico

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Abstract.—*Seepiophila jonesi,* a new genus and species of vestimentiferan tube worm is described from material collected from hydrocarbon seep communities in the Gulf of Mexico, based on morphological and molecular characters. In these communities, individuals occur singly, in small groups or in association with large aggregations of a second vestimentiferan species, *Lamellibrachia* cf. *luymesi.* Tubes extend deeply into the sediment, and a relatively short apical portion normally projects above the sea floor. *Seepiophila jonesi* is most similar to vestimentiferan species in the genus *Escarpia* but differs from it and other vestimentiferan species by a combination of morphological characters that includes the number of types of branchial filaments associated with the branchial plume, the presence of an incision in the posteroventral margin of the vestimentum, the presence of a well-developed, medial obturacular structure, the relative position of the excretory pore and the presence of a variable number of broad collars associated with the tube. The divergence in the sequence of the cytochrome oxidase I gene between *S. jonesi* and other described vestimentiferan tube worms supports its placement in a new genus within the family Escarpiidae.

With the description of *Lamellibrachia barhami,* Webb (1969) recorded the first vestimentiferan tube worm from a cold-water site in the northeastern Pacific Ocean. The discovery of hydrothermal vents and their associated fauna along the Galápagos Rift, East Pacific Rise and Juan de Fuca Ridge of the eastern Pacific Ocean and in various regions of the western Pacific has led to the description of ten additional vestimentiferan species from the Pacific Ocean (Jones 1981, 1985; Southward 1991; Miura et al. 1997; Southward & Galkin 1997; Southward et al. 2001).

In contrast to the Pacific Ocean, the Atlantic Ocean, including the Gulf of Mexico, at present, exhibits much less vestimentiferan diversity. Two species of *Lamellibrachia* are known from putative cold-water sites in the western Atlantic Ocean. Van der Land & Nørrevang (1975) described *L. luymesi* based on a single male specimen taken from about 500 m of water off Guyana, and *L. victori* was characterized by Mañé-Garzón & Montero (1985) based on several specimens dredged from about 300 m of water on the continental slope of Uruguay.

Paull et al. (1984) were the first to report the presence of vestimentiferan tube worms in the Gulf of Mexico. Diving in the submersible *Alvin* at a depth of more than 3000 m at the base of the Florida Escarpment, they observed clumps of specimens that varied in density from a few to more than 100 individuals per square meter. Speci-

Table 1.—Names, coordinates and depths of hydrocarbon seep sites on the Louisiana Slope, Gulf of Mexico sampled for the present study.

Lease block	Site name	Latitude	Longitude	Depth (m)
GC185	Bush Hill	27°47′N	91°31.5′W	540
GC233	Brine Pool	27°43.4′N	91°16.8′W	640
GC234	Green Canyon	27°44.1′N	91°15.3′W	540
TAMU-17	Tamu	27°43.8′N	91°18.2′W	560
GB425	Garden Banks	27°33.3′N	92°32.4′W	570

mens collected from this site were later given the name of *Escarpia laminata* by Jones (1985).

As part of an investigation of the possible effects of hydrocarbon release into overlying waters in the Gulf of Mexico, Kennicutt et al. (1985) performed deep-water trawls at two sites along the Louisiana Slope. One of the trawls contained vestimentiferan specimens which they identified as *Lamellibrachia* sp. Subsequent cruises and submersible dives to sites along the Louisiana Slope revealed the presence of dense assemblages of hydrothermal vent-type taxa, including large aggregations of the vestimentiferan *Lamellibrachia* cf. *luymesi* (see MacDonald et al. 1989, among others). Occurring in association with these aggregations, or sometimes occurring independently, is a second undescribed vestimentiferan species (CRF, SLG, EM pers. obv.). The purpose of the present study is to provide a description of this new species, using morphological features, and to examine its relationships with other vestimentiferans, using morphological and molecular analyses.

Materials and Methods

Specimens were collected by the manned submersibles *Johnson Sea Link I* (*JSL I*) and *Johnson Sea Link II* (*JSL II*) from five seep sites on the Louisiana Slope in the Gulf of Mexico, ranging from 540 to 640 m in depth: Bush Hill, GC234, Brine Pool, TAMU-17 and GB425 (Table 1). Specimens were brought to the surface in a temperature-insulated container and immediately placed in chilled water on board ship. Animals collected for morphological studies were removed from their tubes, preserved in 10% buffered formalin in seawater and subsequently transferred to 70% ethanol. Specimens collected for molecular analyses were removed from their tubes, and a sample of the vestimentum was snipped and immediately frozen in liquid nitrogen. Frozen samples were transported on dry ice and subsequently stored at −80°C.

To show the relationship of the Louisiana Slope vestimentiferans to other known vestimentiferans, we sequenced a portion of the mitochondrial cytochrome oxidase I gene (COI) and compared it with published data for other vestimentiferans (Black et al. 1997, Kojima et al. 1997, Feldman et al. 1998). The four specimens of the new species described herein were collected from four different sites within 65 km of each other on the Louisiana Slope (Bush Hill, GC234, TAMU-17 and GB425). Specimens were stored at −80°C before and after DNA extraction. For these studies, total nucleic acids were extracted from vestimentum tissue by the classic phenol/chloroform extraction technique. The COI gene was amplified by PCR, at an annealing temperature of 55°C, with the following primers: COIf: TC(CA)ACTAATCA(CT) AA(GA) GA-(CT)ATTGG(ATGC)AC, COIr:CC(ATG)-CTTAG(TA)CCTA(GA)(GA)AA (GA)TG-TTG(ATCG)GG (Nelson & Fisher 2000). PCR products were visualized on a 1.5% agarose gel (GIBCO BRL) stained with ethidium bromide. Products were cleaned with a PCR Purification Kit (QIAGEN) before

sequencing. This primer pair amplifies an approximately 1250 base pair segment, from which a 1100 base pair fragment was sequenced with multiple primers, generating overlapping sequences from both strands.

Cycle sequencing PCR was done with a Beckman CEQ DTCS dye terminator reaction kit (BECKMAN), under manufacturer's suggested conditions. End labeled products were separated on a capillary autosequencer (Beckman CEQ 2000XL). Individual sequence runs were assembled and edited with SEQMAN (DNASTAR, Inc.). Consensus sequences generated in this study were aligned (MEGALIGN, DNASTAR Inc.) with those generated in previous studies available in Genbank (Table 2). Molecular evolutionary relationships among sequences were examined by the minimum evolution (ME) method of tree construction (Rzhetsky & Nei 1992) based on pairwise genetic distances estimated from the proportion of differences and corrected for multiple substitutions by the Kimura 2-parameter formula (Kimura 1980). Significance of branching order was evaluated by bootstrap analysis with 1000 replications. Both a pogonophoran from the study of vestimentiferans in Japan by Kojima et al. (1997) and *Galathealinum brachiosum,* a described pogonophoran species, were used as outgroup sequences. All analyses were performed with MEGA (Kumar, version 2.0 beta).

Systematics

The systematic relationships of vestimentiferans (= subphylum Obturata sensu Jones 1981) to pogonophorans (= subphylum Perviata sensu Jones 1981) and to other invertebrate taxa such as the Annelida, as well as their placement in a taxonomic hierarchy, remain unsettled. It is not a purpose of the present study to provide an exhaustive historical account of these issues. Recent morphological, molecular and developmental studies suggest a close relationship between vestimentiferans and pogonophorans and also support an annelid affinity for both groups or place them within the Annelida or Polychaeta (Southward 1988, 1999; Gardiner & Jones 1994; Rouse & Fauchald 1995, 1997; Black et al. 1997; Kojima et al. 1997; McHugh 1997, 2000; Bartolomaeus 1998; Halanych et al. 1998; Rouse 2001). In spite of the seemingly convincing body of evidence provided by these studies, Salvini-Plawen (2000) questioned the reliability of characters used in determining possible relationships between vestimentiferans and pogonophorans and the Annelida-Polychaeta. He concluded that the current level of knowledge of characters of vestimentiferans and pogonophorans is insufficient to provide definitive relationships. Rather, he suggested that, depending on which characters are being analyzed, the two groups demonstrate possible affinities to the Annelida-Polychaeta, Annelida-Oweniidae and Oligomera. He stated that additional comprehensive studies of vestimentiferans and pogonophorans are required to refine better our understanding of their possible relationships with other taxa.

In order to maintain consistency with other recent descriptions of vestimentiferans (Southward 1991, Southward et al. 1995, Miura et al. 1997, Southward & Galkin 1997, Southward et al. 2001), we here adopt the classification proposed by Southward (1991) and consider vestimentiferans as comprising a subclass within the class Pogonophora of the phylum Annelida.

Subclass Obturata Jones, 1981
Order Basibranchia Jones, 1981
Family Escarpiidae Jones, 1985, amended

Diagnosis.—Vestimentiferan worms with tapering tubes and bodies. Anterior obturacular region provided with branchial plume; orientation of branchial lamellae, relative to obturaculum, axial and parallel; branchial filaments of obturacular plume of one type or grouped in two types; plume lacking peripheral lamellar sheaths; anterior

face of obturaculum with moderate to thick crust and usually with variously developed medial structure arising from between obturacular halves; paired internal excretory ducts opening by single, dorsal medial excretory pore near base of obturaculum or more anteriorly, up to one-third distance of obturaculum from base. Anteroventral margin of vestimentum incised, posteroventral margin entire or incised. Opisthosome with setae in single to triple rows. Tube hard, tapering, with or without anterior funnel and variable number of broadly flared external collars and with or without variable number of rings along length.

Remarks.—The family Escarpiidae was amended by Southward et al. (2001) to allow for the inclusion of a new genus and species collected from deep water in the western Pacific Ocean.

The amended diagnosis of the family Escarpiidae provided above is constructed from observations by one of us (SLG) of type specimens of *Escarpia spicata* and *E. laminata* and the new genus and species described herein, together with characters of the new genus described in Southward et al. (2001). The significant morphological feature included in this amended diagnosis is the presence of only a single type of branchial filament associated with the obturacular plume.

Jones (1985) did not possess complete specimens of *Escarpia spicata* or *E. laminata.* Therefore, he was unable to characterize the opisthosome of *Escarpia.* Southward (pers. comm., Southward et al. 2001) describes the opisthosome of one specimen of their new genus as comprising about 15 segments with setae in single to triple rows. Setae are composed of an anterior smaller group of 2–3 teeth and a larger posterior group of teeth occurring in 3–4 rows.

Seepiophila, new genus

Diagnosis.—Vestimentiferan worms with tapering tubes and bodies. Anterior obturacular region provided with branchial plume; orientation of branchial lamellae, relative to obturaculum, axial and parallel; branchial filaments of obturacular plume of one type; plume lacking peripheral lamellar sheaths; anterior face of obturaculum with moderate crust and with conspicuous medial structure arising from between obturacular halves; paired internal excretory ducts opening by single, dorsal medial excretory pore situated on obturaculum approximately one-third distance anteriorly from base. Anteroventral and posteroventral margins of vestimentum incised. Opisthosome unknown. Tube hard, tapering, aperture surrounded by broadly flaring funnel, with variable number of broadly flared external collars anteriorly and with variable number of rings along length.

Type species.—*Seepiophila jonesi,* new species, by present designation.

Gender.—Feminine.

Etymology.—From English *seep* (= a place where water or petroleum oozes out slowly) + Greek *philia* (= affection, fondness), in reference to the strong preference of these worms to inhabit hydrocarbon seep communities in the deep sea.

Seepiophila jonesi, new species
Figs. 1–5

Unidentified vestimentiferan.—Childress et al., 1986:1307.

Undescribed family.—Brooks et al., 1987: 1139, table 1.

Escarpia-like [sic].—Brooks et al., 1987: 1140, table 2, 1141, table 3.

Undescribed member of the family Escarpiidae.—Fisher et al., 1988:230, 232.

Escarpia-like.—MacDonald et al., 1989: 239, 243, table 4.—Childress & Fisher, 1992:382.

The escarpiid.—MacDonald et al., 1989: 241, 245, fig. 3B.

Escarpia sp. [not *Escarpia* Jones, 1985].—MacDonald et al., 1989:235.—Young et al., 1996:514–516, figs. 1b, 2a, c, f-1.—Miura et al., 1997:455.—Southward, 1999:196.—Tyler & Young, 1999:197,

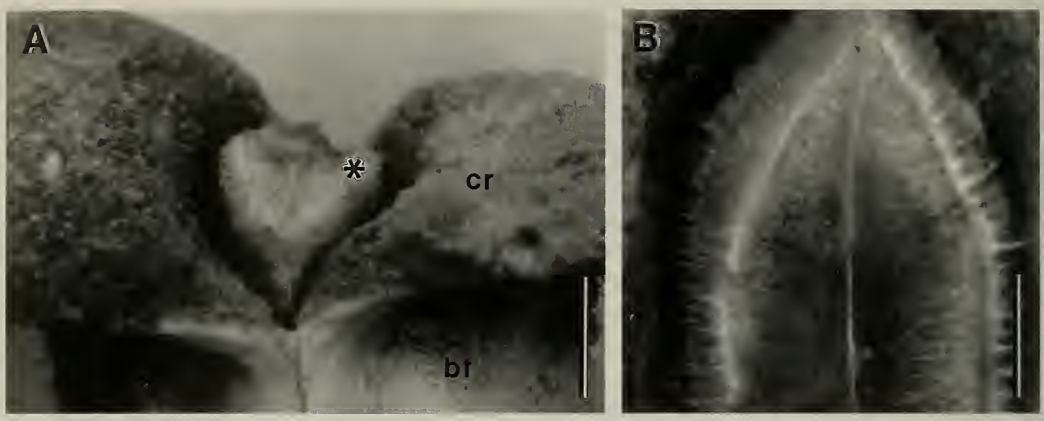

Fig. 1. *Seepiophila jonesi,* new species. Holotype (USNM 188519). A, Anterior face of obturaculum showing crust-like material (cr) and prominent medial process (asterisk). bf, branchial filaments. B, Enlargement of portion of medial process. Note numerous spines along lateral margins. Scale bars: A = 2 mm; B = 1 mm.

table 3, 198.—Salvini-Plawen, 2000:133, 134.

Undescribed genus.—Fisher, 1990:406, table 1, 410.

Unidentified escarpid.—Fisher et al., 1990: 1095, table 1.

E. sp. [not *Escarpia* Jones, 1985].—Fisher, 1995:307, table 4.

Escarpiidae species.—Nelson & Fisher, 1995:128, table 1.

Escarpia spicata [not *Escarpia spicata* Jones, 1985].—Feldman et al., 1997:270.

Escarpid-like.—Fisher et al., 1997:83–94, fig. 1b (as escarpids).—Nelson & Fisher, 2000:1–10.

Undescribed seep escarpid.—Scott et al., 1998:379, table 1.

Type material.—See Table 1 for coordinates and depths of hydrocarbon seep communities. Holotype, (USNM 188519), 6 paratypes (USNM 188520–188525), Bush Hill hydrocarbon seep community, *JSL I* Dive 3775, 8 Oct 1994, coll. S. L. Gardiner; 6 paratypes, Bush Hill hydrocarbon seep community, *JSL I* Dive 3530, 28 Jun 1993, coll. J. J. Childress. Additional type material is deposited in the Natural History Museum, London, the Canadian Museum of Nature, the National Science Museum, Tokyo and the Muséum National d'Histoire Naturelle, Paris.

Additional material examined.—See Table 1 for coordinates and depths of hydrocarbon seep communities. For morphological analyses: 14 specimens, Green Canyon hydrocarbon seep community, *JSL I* Dive 3525, 26 Jun 1993, coll. E. Nix; 2 specimens, Green Canyon hydrocarbon seep community, *JSL I* Dive 3526, 26 Jun 1993, coll. J. J. Childress; 8 specimens, Bush Hill hydrocarbon seep community, *JSL I* Dive 3530, 28 Jun 1993, coll. J. J. Childress; 17 specimens, Bush Hill hydrocarbon seep community, *JSL I* Dive 3775, 8 Oct 1994, coll. S. L. Gardiner. For molecular analyses: 1 specimen, Bush Hill hydrocarbon seep community, *JSL II* Dive 2853, 10 Jul 1997, coll. K. Nelson; 1 specimen, Green Canyon hydrocarbon seep community, *JSL II* Dive 2866, 16 Jul 1997, coll. K. Nelson; 1 specimen, Garden Banks hydrocarbon seep community, *JSL I* Dive 4053, 17 Jul 1998, coll. E. McMullin; 1 specimen, TAMU-17 hydrocarbon seep community, *JSL I* Dive 4049, 15 Jul 1998, coll. E. McMullin.

Diagnosis.—Characters of the genus.

Etymology.—The species is named in honor of the late Meredith L. Jones whose studies of vestimentiferan anatomy, morphology and development contributed greatly to our understanding of this enigmatic group of marine worms.

Description.—Measurements of selected specimens (length by diameter, in mm; obturacular: vestimental: trunk: opisthosomal regions; + = incomplete; − = change in diameter; — = missing); (USNM 188519): 9.5 by 7.5: 36.4 by 10.2: 415+ by 5.9–0.4: —; (USNM 188520): 12.1 by 7.8: 44.2 by 8.9: 330+ by 6.4–1.6: —; (USNM 188521): 11.5 by 6.1: 38.7 by 7.5: 100+ by 4.5–3.5: —; (USNM 188522): 10.7 by 6.1: 45.1 by 6.5: 380+ by 6.4–0.8: —; (USNM 188525): 11.2 by 5.6: 52.1 by 7.4: 350+ by 4.7–1.0: —). Measurements of selected tubes: (USNM 188519): 870+ by 12.4–1.0; (USNM 188520): 955+ by 9.6–0.8; (USNM 188523): 810+ by 11.6–0.6; (USNM 188524): 820+ by 10.9–2.7.

Anterior face of obturaculum with moderately developed crust, up to approximately 1 mm in thickness (Fig. 1A); cuticular axial rod between obturacular halves of distal one-third of obturaculum, extending beyond anterior face of obturaculum as prominent medial structure, laterally compressed, terminating bluntly, lateral margins provided with numerous small spines (Fig. 1A, B); measurements of selected medial structures (anteroposterior length above anterior face of obturaculum by dorsoventral height by lateral width) in mm: (USNM 188519): 1.5 by 5.9 by 3; (USNM 188521): 1.6 by 4.7 by 2.3; (USNM 188523): 1.5 by 5.5 by 2.5; (USNM 188525): 0.8 by 4.5 by 1.7. Obturaculum with approximately 45–50 pairs of branchial lamellae (Fig. 2A–D), lacking specialized sensory filaments; filaments comprising lamellae of one type, fused for greater portion of length, with single row of pinnules extending along free portion of filaments (Fig. 3A) and with two rows of ciliated cells (Fig. 3A, B); pinnules on filaments of lamella one (= oldest lamella) relatively inconspicuous, often irregularly spaced along distal length of filaments (Fig. 3C); pinnules on filaments of middle and posterior-most lamellae larger, regularly spaced along distal length of filaments (Fig. 3A, B); midventral face and distal sides of obturaculum bare; obturaculum laterally compressed at base, oval to somewhat spindle-shaped in cross-section more distally (Fig. 4A), lacking dorsal groove, with poorly developed ventral ridge; paired internal excretory ducts (Fig. 4A) opening by single pore on dorsal medial ridge approximately one-third distance of obturaculum from base (Fig. 2D, arrow), dorsal medial ridge sometimes darkly pigmented; ratio of obturacular length to vestimental length variable, 1:2.8 to 1:6.6. Anterior margin of vestimentum forming short sheath around base of obturaculum (Fig. 2A), with shallow midventral incision often forming small lobes (Fig. 2C); posteroventral margin of vestimentum deeply incised, with two conspicuous lobes (Fig. 2C, large arrowhead, E); ratio of vestimental diameter to vestimental length highly variable, 1:3.1 to 1:12.6; ventral surface with tear-drop shaped ciliated field; plaques associated with epidermis ventrolaterally (Fig. 2E, arrowhead); males with paired dorsal ciliated grooves extending from gonopores to near anterior end of vestimentum, converging slightly anteriorly (Fig. 2D, arrowheads). Trunk very long in adult specimens, tapering to less than 1 mm in diameter; epidermis with numerous associated plaques (Fig. 2E, arrowhead). Opisthosome unknown. Tube hard, often somewhat darkly colored, tapering posteriorly, aperture with broadly flaring funnel (Figs. 4B, 5); diameter of aperture variable (6.6–11 mm; $\bar{X} = 9.1 \pm 1.3$ mm, $n = 34$), with variable number of collars posterior to aperture (0–10; $\bar{X} = 3.2 \pm 1.9$, $n = 34$); number of rings posterior to aperture highly variable (11–59; $\bar{X} = 29.8 \pm 10.2$, $n = 34$).

Distribution.—Presently known only in association with certain hydrocarbon seep communities in the Gulf of Mexico between 500 and 1000 m depth.

Remarks.—Seven vestimentiferan species in six genera possess a medial structure in association with the obturaculum: *Escarpia spicata* Jones, 1985, *E. laminata* Jones, 1985, *Oasisia alvinae* Jones, 1985, *Ridgeia piscesae* Jones, 1985, *Tevnia jerichonana*

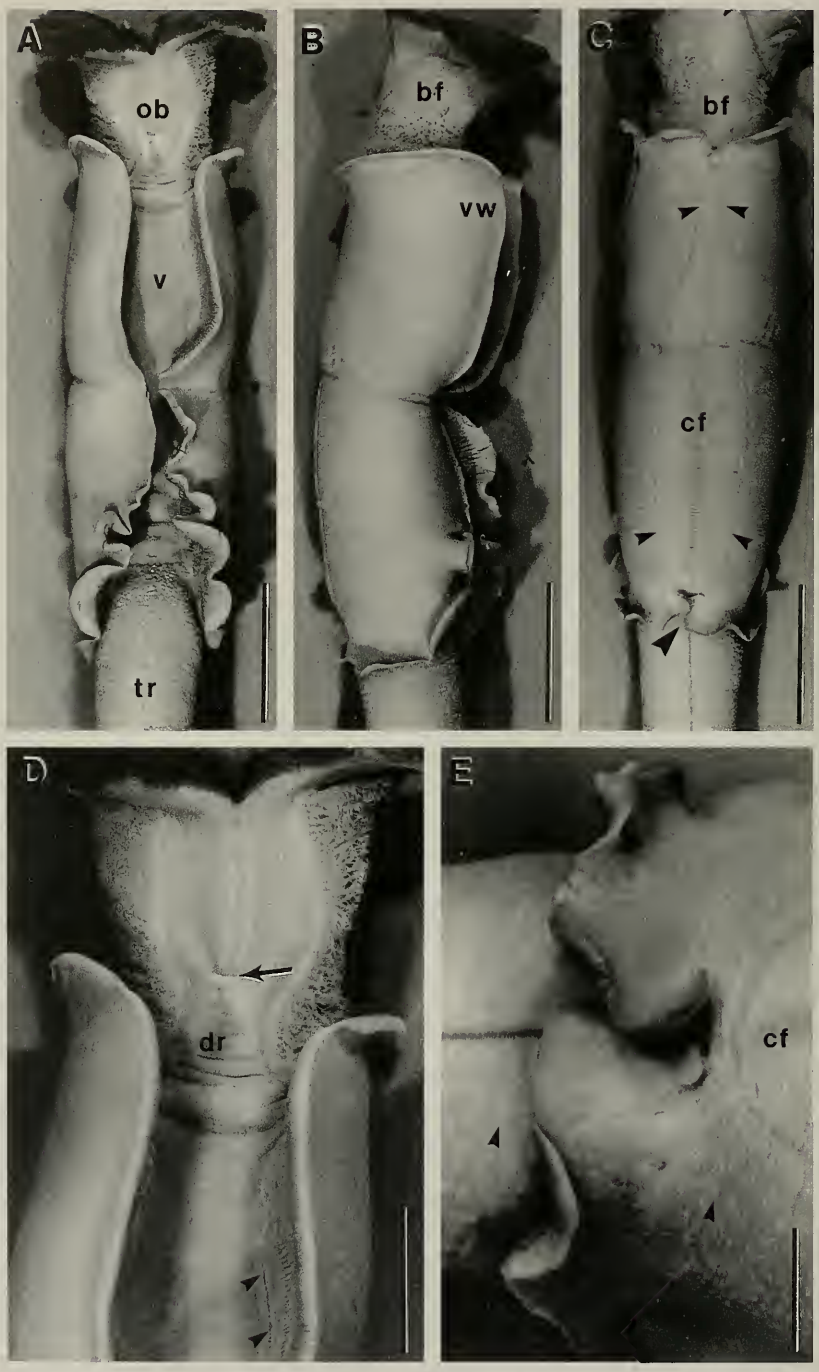

Fig. 2. *Seepiophila jonesi,* new species. Holotype (USNM 188519). A, Dorsal view of obturacular (ob) and vestimental (v) regions and portion of trunk region (tr). Note broadly splayed anterior face of obturaculum. B, Left lateral view of obturacular region showing branchial filaments (bf), vestimental region with vestimental wings (vw) and portion of trunk. C, Ventral view of obturacular region, vestimental region with tear-drop shaped ciliated field (cf) and portion of trunk region. Small arrowheads indicate position of intraepithelial nerve cords. Note deeply incised posteroventral margin of vestimentum (large arrowhead). bf, branchial filaments. D, Enlarged dorsal view of obturacular region showing prominent dorsal ridge (dr) at base of obturaculum. Arrow indicates

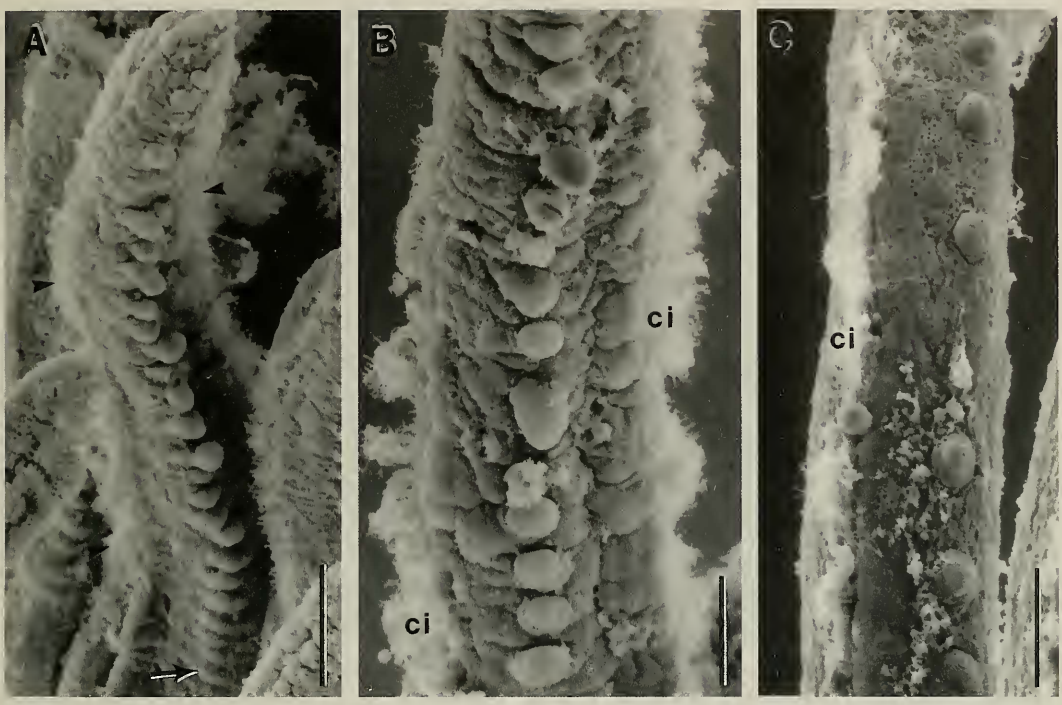

Fig. 3. *Seepiophila jonesi,* new species. Scanning electron microscopy. Non-type specimens. A, Branchial filament from middle lamella. Single row of pinnules extends from near tip of filament to region where filament fuses with adjacent filaments. Note diminished size of pinnules in region of fusion (arrow). Arrowheads indicate cilia. B, Branchial filament from basal lamella. Note well-developed pinnules and two rows of ciliated cells (ci). C, Branchial filament from lamella one (= oldest lamella). Note single row of small, somewhat irregularly spaced pinnules. ci, cilia. Scale bars: A = 50 μm; B = 25 μm; C = 30 μm.

Jones, 1985, a new genus described in Southward et al. (2001) and *Seepiophila jonesi,* new species. *Seepiophila jonesi,* however, differs from all other species that possess an obturacular medial structure in having only a single type of filament comprising the branchial lamellae. In *S. jonesi,* all filaments possess a single row of pinnules, whereas other species that display an obturacular medial structure possess at least some filaments that lack pinnules.

A crust-like material on the anterior face of the obturaculum and a medial structure secreted by the obturacular halves are characters shared by all species in the Escarpiidae. The crust-like material appears to be about equally developed in the four species of the family. This is not the case, however, for the medial structure. Jones (1985) did not report dimensions for the medial structure of *Escarpia laminata,* presumably because of its small size. He reported, however, that the medial structure of *E. spicata* extends as much as 9.5 mm above the anterior face of the obturaculum. Southward (pers. comm.) indicates that one specimen of their new genus (Southward et al. 2001) possesses a medial structure that extends 20

←

approximate position of excretory pore. Note ciliated groove on dorsal surface of vestimentum (arrowheads). E, Enlarged view of posteroventral margin of vestimentum showing lobed condition. Arrowheads indicate plaques associated with epidermis of vestimentum and trunk. cf, ciliated field. Scale bars: A–C = 10 mm; D = 5 mm; E = 2 mm.

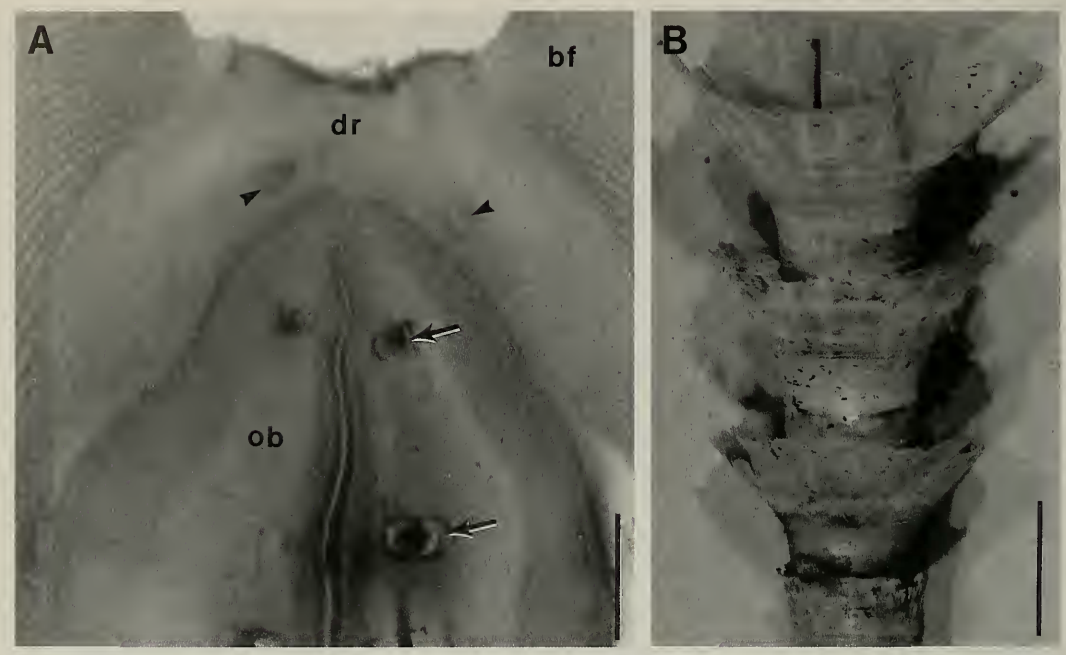

Fig. 4. *Seepiophila jonesi,* new species. A, Non-type specimen. Light microscopic view of transverse section through obturacular region. Small arrowheads indicate positions of paired excretory ducts. Arrows indicate sections through obturacular blood vessel. bf, branchial filaments; dr, dorsal ridge; ob, obturacular half. B, Anterior region of tube showing aperture surrounded by broadly flaring funnel and two well-developed collars posterior to aperture. Scale bars: A = 0.5 mm; B = 10 mm.

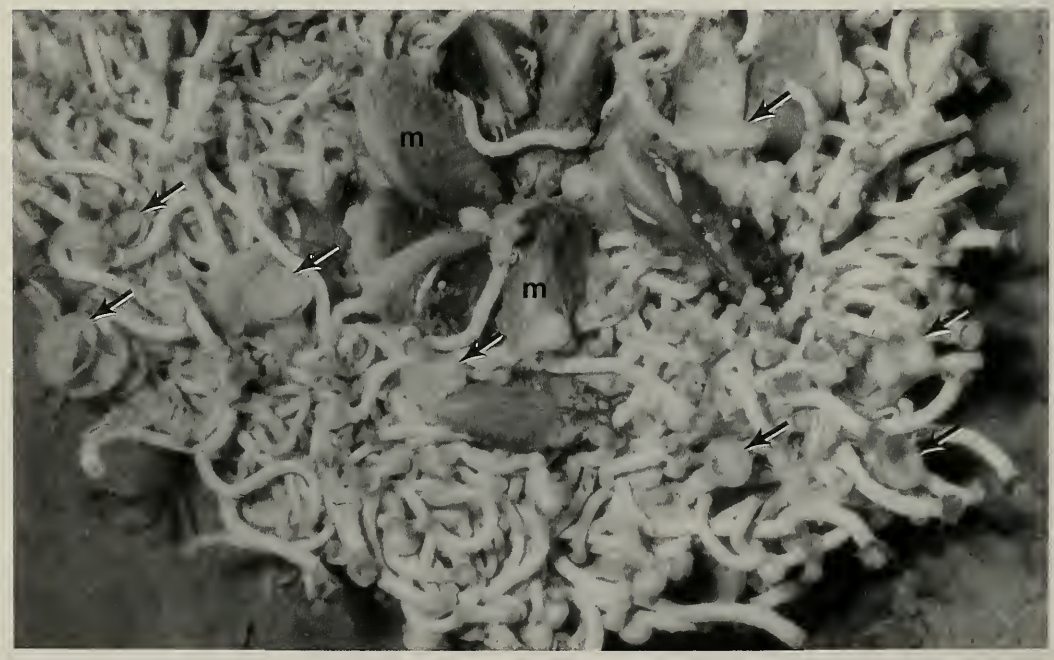

Fig. 5. Individuals of *Seepiophila jonesi* (arrows) within a clump of juvenile specimens of *Lamellibrachia* cf. *luymesi* and several seep mussels (m). No scale.

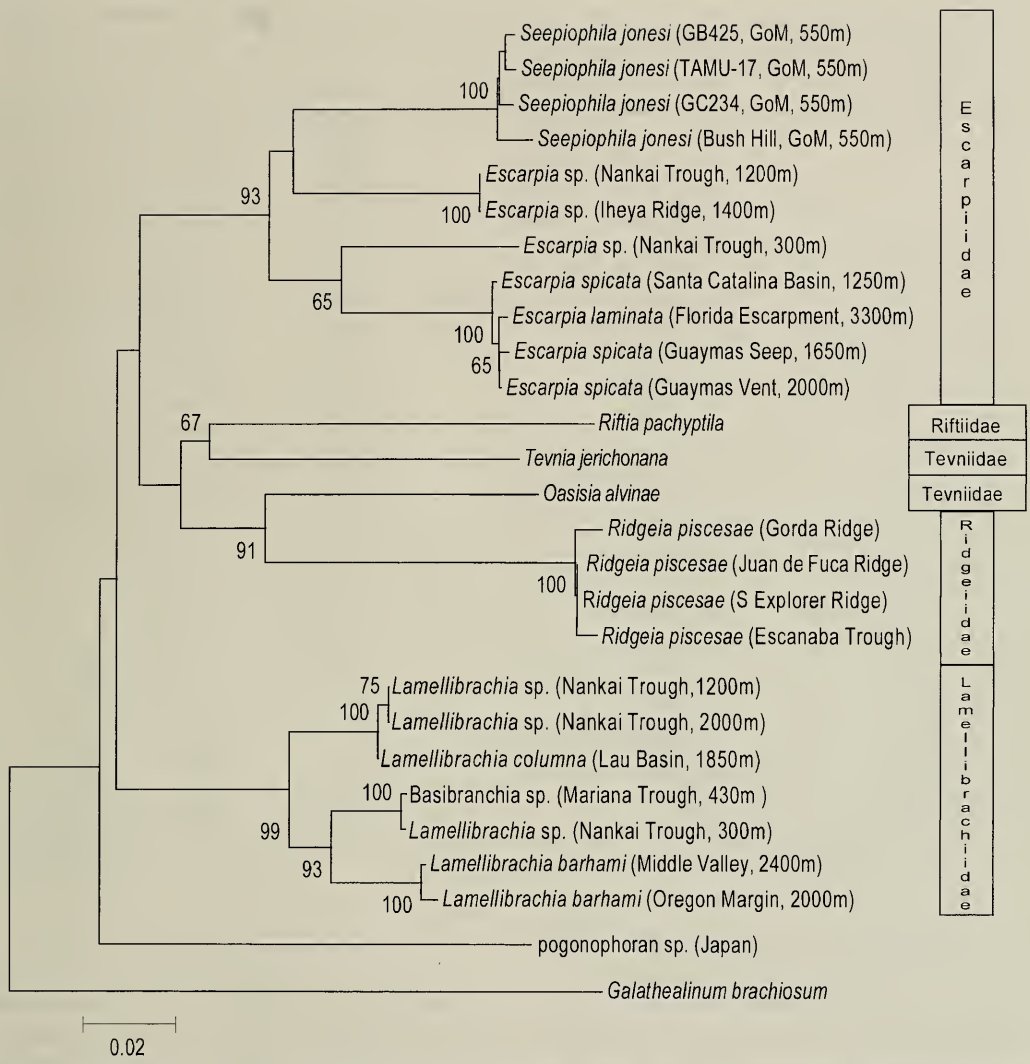

Fig. 6. Minimum evolution tree showing the relationships among tube worms based on a partial sequence (500 base pairs) of the mitochondrial cytochrome oxidase I gene, using the Kimura 2-parameter correction for multiple substitutions (references and Genbank accession numbers shown in Table 2). Numbers at nodes indicate the proportion of occurrences of a particular branching order in 1000 bootstrap replications. Bootstrap values below 65 not shown. GoM, Gulf of Mexico.

mm beyond the anterior face of the obturaculum. While the medial structure of *Seepiophila jonesi* is prominent and readily visible, it does not project a great distance beyond the anterior face of the obturaculum. The greatest distance recorded in specimens available for this study was 3.5 mm. Also, the medial structure of *S. jonesi* ends bluntly, whereas those of the new genus (Southward et al. 2001) and *E. spicata* taper to a sharp point or terminate in a slightly bifid tip, respectively.

Paired internal excretory ducts opening through a single pore is a feature *Seepiophila jonesi* shares with other species in the Escarpiidae. However, in addition to having only a single type of filament associated with its branchial lamellae, the posteroven-

Table 2.—Collection locations, GenBank accession numbers and references for vestimentiferan specimens used in the present analysis of the COI gene.

Organism	Location	GenBank accession	Reference
Escarpia laminata	Florida Escarpment	U74063	Black et al. 1997
Escarpia sp.	Nankai Trough (300 m)	D50593	Kojima et al. 1997
Escarpia sp.	Nankai Trough (1200 m)	D50594	Kojima et al. 1997
Escarpia sp.	Iheya Ridge (1400 m)	D50595	Kojima et al. 1997
Escarpia spicata	Guaymas Basin seep	U74065	Black et al. 1997
Escarpia spicata	Guaymas Basin vent	U74064	Black et al. 1997
Escarpia spicata	Santa Catalina Basin whale fall	U84262	Feldman et al. 1998
Basibranchia sp.	Mariana Trough	U74078	Black et al. 1997
Lamellibrachia barhami	Middle Valley	U74055	Black et al. 1997
Lamellibrachia barhami	Oregon margin	U74054	Black et al. 1997
Lamellibrachia columna	Lau Basin	U74061	Black et al. 1997
Lamellibrachia sp.	Nankai Trough (1200 m)	D38029	Kojima et al. 1997
Lamellibrachia sp.	Nankai Trough (300 m)	D38030	Kojima et al. 1997
Lamellibrachia sp.	Nankai Trough (2000 m)	D50592	Kojima et al. 1997
Oasisia alvinae	21°N Eastern Pacific Rise	U74069	Black et al. 1997
Seepiophila jonesi	Gulf of Mexico, Bush Hill	AF317287	This study
Seepiophila jonesi	Gulf of Mexico, GB425	AF317288	This study
Seepiophila jonesi	Gulf of Mexico, GC234	AF317289	This study
Seepiophila jonesi	Gulf of Mexico, TAMU-17	AF317290	This study
Ridgeia piscesae	Southern Explorer Ridge	U74057	Black et al. 1997
Ridgeia piscesae	Juan de Fuca Ridge	AF022233	Black unpublished
Ridgeia piscesae	Gorda Ridge	U87978	Black et al. 1998
Ridgeia piscesae	Escanaba Trough	AF022235	Black unpublished
Riftia pachyptila	9°N Eastern Pacific Rise	U74074	Black et al. 1997
Tevnia jerichonana	9°N Eastern Pacific Rise	U74075	Black et al. 1997
pogonophoran sp.	Japan	D50598	Kojima et al. 1997
Galathealinum brachiosum	Oregon	AF178679	Boore & Brown 2000

tral margin of the vestimentum is deeply incised in *S. jonesi,* whereas this margin is entire in species of *Escarpia. Seepiophila jonesi* and species of *Escarpia* also differ in the relative position of the excretory pore. Jones (1985) states that the excretory pore is situated near the base of the obturaculum in *Escarpia,* whereas in *S. jonesi* it is positioned approximately one-third the distance from the base to the apex of the obturaculum.

Collars associated with tubes is a widespread feature among basibranchian vestimentiferans, and therefore, we believe this characteristic should not be emphasized in comparative accounts. However, it is worthy of note that the tubes of *Seepiophila jonesi* possess well-developed collars, whereas such collars are not present on tubes of species of *Escarpia.*

Discussion

Presently, 15 species of vestimentiferan tube worms have been recognized and described (Webb 1969; van der Land & Nørrevang 1975; Jones 1981, 1985; Mañé-Garzón & Montero 1985; Southward 1991; Miura et al. 1997; Southward & Galkin 1997). *Ridgeia phaeophiale,* originally described by Jones (1985), was subsequently synonymized with *R. piscesae* by Southward et al. (1995). Of the remaining 14 species, eight species are reported only from hydrothermal vent communities, including *Riftia pachyptila, Oasisia alvinae, Tevnia jerichonana, Ridgeia piscesae, Alaysia spiralis, Lamellibrachia columna, L. satsuma* and *Arcovestia ivanovi.* Four species are known exclusively from cold-water communities, including *L. barhami, L. luy-*

mesi, L. victori, and *Escarpia laminata. Escarpia spicata* is reported from cold-water and hydrothermal vent sites (Jones 1985, Black et al. 1997). *Seepiophila jonesi,* at present, represents an additional species occurring only in cold-water communities.

The recognition of *Seepiophila jonesi* raises the number of vestimentiferan species known from the Gulf of Mexico to three. *Lamellibrachia* cf. *luymesi* and *S. jonesi* are sympatric in all of the shallow water hydrocarbon seep communities sampled for this study. The third species, *Escarpia laminata,* is currently recorded only from deep water at the base of the Florida Escarpment (Jones 1985).

In order to further clarify the phylogenetic position of *Seepiophila jonesi* among other vestimentiferans, we conducted an analysis of the mitochondrial COI gene in specimens of the genera *Seepiophila, Escarpia, Riftia, Tevnia, Oasisia, Ridgeia,* and *Lamellibrachia* (see Table 2). The average divergence for the COI gene among the four specimens of *S. jonesi* from the Louisiana Slope was low (0.8%), whereas the average divergence among the vestimentiferans in the escarpid cluster was 7.6%. As a comparison, sequence divergence within the described group of *L. barhami* is 0.3%, and the divergence among the lamellibrachids is 4.5%. This difference in divergence is reflected in the deeper branches between species of the escarpid cluster than those of the lamellibrachid group (Fig. 6). The very low sequence divergence among the samples of *S. jonesi* suggests that the four individuals (found within 65 km of each other) are members of a single, freely interbreeding species. The very deep branching pattern between *S. jonesi* and other species in the family Escarpiidae is a reflection of the relatively high degree of sequence divergence between *S. jonesi* and the remaining species of the Escarpiidae. Although no definitive "molecular clock" exists that could generate benchmarks for the naming of genera, families, etc., the deep branching pattern within the Escarpiidae relative to that within the Lamellibrachiidae supports the placement of the Louisiana Slope vestimentiferans within a new genus but still within the larger cluster of the family Escarpiidae.

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